Origin of Phytophthora cinnamomi: Evidence That It is Not an Indigenous Fungus in the Americas

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It is with pleasure that I acknowledge the invaluable assistance in collecting *Persea* spp. in Latin America of many individuals and many organizations including personnel in the Ministries of Agriculture, Experiment Stations, and Universities, in most of the countries listed and the Rockefeller Foundation in Mexico; also the technical assistance in California of W. A. Thorn.

Research in recent years supported in part by grants from the California Avocado Advisory Board.

Accepted for publication 16 May 1977.

ABSTRACT

ZENTMYER, G. A. 1977. Origin of Phytophthora cinnamomi: Evidence that it is not an indigenous fungus in the Americas. Phytopathology 67: 1373-1377.

Cultures were made from roots from 373 native *Persea* trees and cultivated avocado trees (*Persea americana*) in 18 countries including Mexico and countries in Central and South America and the Caribbean. The root samples were collected from 11 species and varieties of *Persea* and from five other related genera in the Lauraceae. *Phytophthora cinnamomi* was not recovered from any trees in native, undisturbed sites, or from undisturbed soils in southern California avocado areas, but was readily recovered from roots of trees brought into cultivation and affected with root rot. These data indicate that it is unlikely that *P. cinnamomi* is an indigenous fungus in the Americas.

Additional key words: avocado, *Persea*.

There has been considerable speculation in recent years regarding the possible origin of the cosmopolitan plant pathogen, *Phytophthora cinnamomi* Rands. This paper presents additional information relating to this matter, particularly on the possibility that *P. cinnamomi* might be indigenous in the Americas.

Newhook and Podger (10) discussed the origin of *P. cinnamomi* at length, and concluded that the fungus had been introduced into the Australia-New Zealand area probably no earlier than the late 18th century. Additional information has been presented since that time in relation to Australia, by Pratt and Heather (13), Pratt et al. (14) and Brown (2), indicating that the fungus may be indigenous to eastern Australia.

Shepherd (16) recently presented a comprehensive analysis of the possible origin of *P. cinnamomi* and concluded that the fungus entered northern Australia with "..Indo-Malasian floristic elements during Pleistocene-Holocene times from a centre of origin in the New Guinea-Celebes region". The recovery of *P. cinnamomi* from native Nothofagus forest in New Guinea by Shaw et al. (15) in 1973 adds support to Shepherd's hypothesis.

Crandall and Gravatt (6) proposed that *P. cinnamomi* was introduced into various southern ports in the United States, probably in the 18th century, and speculated that the pathogen had its origin in Asia. Campbell (3) and Hendrix et al. (8) have presented some data to the contrary on this point, suggesting that *P. cinnamomi* may be indigenous to the southeastern United States. Campbell isolated the pathogen from 31 of 61 plots in healthy pine stands in Alabama, Florida, Georgia, Mississippi, and South Carolina, noting that the fungus occurred "... in places remote from any known connection with a recognized disease". Hendrix et al. (8) recovered *P. cinnamomi* from one (in Tennessee) of eight "remote" areas sampled in old growth areas in Kentucky, North Carolina, and Tennessee, stating that these were locations was limited trails. They concluded that *P. cinnamomi* "..may have been indigenous to the South, and not entirely an introduced species". No data have been presented on the possible origin of the fungus in California where it has been a serious problem especially on avocado for at least 30 yr.

Information on the origin of *P. cinnamomi* is significant in regard to disease prevention and control. If *P. cinnamomi* is not native to the areas in southern California where avocado trees are planted, exclusion of the fungus from new plantings by all possible means (i.e., clean nursery stock, prevention of soil and water movement from infested areas, etc.) becomes highly significant (25).

In connection with studies of the biology and control of *P. cinnamomi* in relation to avocado root rot over the past 25 yr, attempts have been made to determine if the fungus is indigenous in southern California and also in Latin America. This paper reports the results of these cultures and related tests.

MATERIALS AND METHODS

California.—Soil samples were taken in areas of native chaparral in Los Angeles, San Diego, and Santa Barbara counties in southern California, with emphasis on small arroyos and drainage areas that retained some moisture during the dry season. Samples were taken above

TABLE 1. Isolation of *Phytophthora cinnamomi* from root samples collected from native species of *Persea* and from cultivated avocado trees in Mexico, Central and South America, and the Caribbean

Country	Native species of *Persea*[a] and related Lauraceae	Avocado trees under cultivation: No. of samples	Avocado trees under cultivation: No. with *P. cinnamomi*
Argentina		14	3
Brazil	*P. alba* (1)[b]	5	2
Chile	*P. lingue* (2) *Beilschmedia miersii* (2)[c]	11	6
Colombia	*P. americana* (1)	3	0
Costa Rica	*P. americana* (3) *P. schiedeana* (2) *P. caerulea* (1) (*P. skutchii*) *Phoebe mexicana* (1)[c]	19	15
Cuba		1	1
Ecuador		6	0
El Salvador	*P. americana* (2) *P. schiedeana* (2)	8	5
Guatemala	*P. americana* v. *nubigena* (2) (*P. nubigena*) *P. donnell-smithii* (2) *P. schiedeana* (14)[d] *P. steyermarkii* (1) *Aouiea* sp. (1)[c]	42	0
Haiti		2	1
Honduras	*P. americana* v. *gigantea* (2) (*P. gigantea*) *P. caerulea* (2) (*P. skutchii*) *P. donnell-smithii* (1) *P. vesticula* (1) (*P. popenoei*) *Nectandra sinuata* (1)[c]	51	19
Mexico	*P. americana* (10) *P. schiedeana* (5)[d]	101	16
Peru	*P. subcordata* (1) (*P. durifolia*) *Ocotea* sp. (1)[c]	3	2
Puerto Rico		41	14
St. Croix		2	1
Trinidad		1	1
Venezuela	*P. caerulea* (1)	...[e]	...

[a]Classification of *Persea* spp. based on Kopp (9). Nomenclature when collection was made is indicated in parentheses; based on collections in various herbaria. Number of samples is indicated in parentheses.

[b]Number of trees sampled. These were negative for *Phytophthora cinnamomi* with two exceptions, see "d" below.

[c]Genus in the family Lauraceae related to *Persea*.

[d]*Phytophthora cinnamomi* isolated from one tree, not in undisturbed situation.

[e]No avocado samples were taken.

cultivated areas to minimize the opportunity of infestation of the areas from avocado groves or other possible sources of inoculum. Roots from these samples were cultured on cornmeal agar (prior to the advent of antibiotic media for isolation of *Phytophthora*); some more recent samples were cultured on PV and $P_{10}VP$ media (17). On these media, *P. cinnamomi* can readily be recovered from diseased roots, by selecting small absorbing roots 1 to 2 mm in diameter that are necrotic (usually with a black, brittle rot extending through the root) or have brown to black lesions. Small pieces of these roots approximately 1 cm in length are rinsed in water, dipped briefly in 70% alcohol, blotted on a paper towel or filter paper, and pressed into the agar.

Approximately 30% of the soil samples were placed in clay pots or other containers in the glasshouse, planted with avocado seedlings susceptible to *P. cinnamomi*, and the seedlings were grown for several months. These soils were watered frequently to maintain moisture conditions favorable for the development of *Phytophthora*, if present.

Latin America.—In the course of a number of trips to Mexico, Central and South America, and the Carribean over the past 25 yr, in the search for species of *Persea* resistant to *Phytophthora cinnamomi* (19, 20, 21), root samples have been collected in many areas where species of *Persea* are native. *Persea* (the avocado is *P. americana* Mill.) is primarily an American hemisphere genus, with over 80 species native from the southern United States to Chile (9).

As with the California samples, necrotic roots were cultured on cornmeal agar or on cornmeal agar containing antibiotics usually the same day as collected, using pre-poured plates taken with me. Plates were examined as a rule in 3 to 5 days, using various experiment station or University facilities.

In the Latin America countries, root samples also were taken where the avocado has been brought into cultivation in many of the countries. Root samples have been collected in Argentina, Brazil, Chile, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Puerto Rico, St. Croix (Virgin Islands), Trinidad, and Venezuela.

RESULTS

From over 300 soil and root samples collected in southern California from undisturbed areas above possible sources of infestation, over a period of several years, no *Phytophthora cinnamomi* was recovered. No root rot developed on the avocado seedlings planted in these soils, nor was *Phytophthora cinnamomi* recovered from a few rotted roots of these plants at the time that the root systems were washed from the soil on termination of the tests. *Phytophthora cinnamomi* was recovered from one sample from a small arroyo containing native vegetation; this was below an area where avocado trees were affected with Phytophthora root rot and the fungus undoubtedly was carried into the arroyo area by drainage water.

Results of culturing roots from 373 trees from 18 countries in Latin America are presented in Table 1. In no case was *P. cinnamomi* recovered from any native trees of *Persea* growing in an undisturbed area, even though a number of the samples were taken in rain forests and swamps, in areas of very high rainfall and in soils containing considerable clay–situations in which *P. cinnamomi* would be expected to develop and conditions under which it could be easily cultured if present. No diseased trees were seen under native, undisturbed soil conditions in any of the countries where samples were taken.

Phytophthora cinnamomi was isolated from four trees not growing in a formal grove situation in Latin America: (i) from two avocado trees (*Persea americana*) growing in coffee plantings in the State of Veracruz, Mexico; (ii) from a roadside tree of *Persea schiedeana* in the State of Veracruz, Mexico; and (iii) from a tree of *P. schiedeana* growing at the edge of a cornfield near the village of San Pedro Carcha, Alta Verapaz, Guatemala. In none of these cases could importation of the fungus on other plants be ruled out, as cultivated crops were nearby; these were not in indigenous forest situations.

Phytophthora cinnamomi was recovered from many avocado trees affected with Phytophthora root rot in most of the countries in Latin America (Table 1); these were trees brought into cultivation, or in semi-cultivation in small groves, or in local fence-row or garden plantings for food production. Many of these isolates have been included in our *Phytophthora* culture collection, and are being used for studies of variability in this species.

DISCUSSION AND CONCLUSIONS

Thus, to date, *P. cinnamomi* has not been isolated from undisturbed soils in California nor from indigenous species of *Persea* growing in undisturbed localities in the Americas. The data indicate that it is very unlikely that this pathogen is a native fungus in soils in southern California. This information is substantiated by the fact that in a number of cases where the fungus has been found in new plantings in soil cleared of native vegetation, the infection has been traced to infected nursery stock, with subsequent spread out from these centers (Zentmyer, *unpublished*). This occurrence is much less common than formerly, with use of measures to produce nursery stock free from *P. cinnamomi* (25). The climate of southern California would not favor *P. cinnamomi* as a native inhabitant of the soil, since prior to the advent of irrigated agriculture a fungus of this type probably could not have survived the periodic long, hot, dry periods, with little or no rainfall from April to November.

The situation in the southeastern United States appears to warrant further study. Campbell's (3) isolation of *P. cinnamomi* in the southeast in places remote from any connection with a recognized disease is certainly not conclusive evidence of the indigenous nature of the fungus, as it could have been transported to such areas by many means. Was the one area in Tennessee from which Hendrix et al. (8) isolated *P. cinnamomi* a truly undisturbed site, with no possibility of movement in years past of a fungus from elsewhere, by activities of man or by animals or water movement? This seems questionable in a country that has been inhabited for so many years, but is certainly worth further examination. Also, details regarding the *P. cinnamomi* isolate could be of significance; Hendrix et al. made no comment on the fungus. Was it a "typical" *P. cinnamomi* culture,

morphologically and physiologically, pathogenic to pine and other hosts?

The data from various countries in Latin America indicate that the fungus may not be native in those areas, but more detailed surveys are necessary before definite conclusions can be reached on this point. The possibility still exists that a very low population of *P. cinnamomi* may be present in some of the native soils and may not be detected even on selective antibiotic media. Culture of a susceptible host in such soils, such as was done with the California samples, or the use of various "baiting" techniques, might result in detection of the pathogen.

It seems likely that *P. cinnamomi* was imported into California from tropical America and/or possibly from Hawaii in the late 19th century or early in this century, in connection with importations of avocado or other subtropical or tropical plants. In the early days of the avocado industry in California, avocado seeds and seedlings commonly were brought or sent to southern California from Mexico, Guatemala, and other tropical areas prior to quarantine restriction on soil and plant material. Popenoe in 1912 (11) mentioned that avocado seeds had been brought to California from Mexico and Guatemala. In 1916 Condit (4) quoted Dr. Franceschi, an early grower of subtropical crops in Santa Barbara, southern California, who stated that the first avocado trees were brought to California from Mexico in 1871. Of possible significance is Dr. Franceschi's report that "One of these trees died in infancy...while another died later, probably on account of the ground being too shallow and dry...". This could have been the first instance of introduction of *P. cinnamomi*, as well as the avocado, into California. Dr. Franceschi also noted that an avocado tree that he saw in Los Angeles in 1892 had been brought from Guatemala, "...together with many other rare and interesting trees...". This indicates the ease with which plant material was imported at that time. Condit (5) later listed a number of avocado selections that had been introduced into California as seedling trees or seeds from Mexico, Guatemala, and Costa Rica, and listed other introductions from Cuba, Ecuador, Samoa, and Venezuela. The pathogen could have been transported in soil accompanying plants or in seed, if seed came from fruit that had fallen on soil infested with *P. cinnamomi.*

Phytophthora cinnamomi has been present for many years in a number of locations in Mexico where avocados have been under cultivation or semicultivation as scattered producing trees; one such area is Atlixco, in the State of Puebla, the origin of many of the original California avocado importations. Another noted avocado center is Queretaro, State of Queretaro; Phytophthora root rot by 1960 had nearly eliminated the thousands of avocado trees that were common in this area in the 1920's and 1930's. Importation of the pathogen from Guatemala is extremely unlikely even though this country ranks with Mexico as one of the important sources of avocado materials imported into California beginning with the exploration of Wilson Popenoe 60 years ago (12). *Phytophthora cinnamomi* has never been found on avocado in Guatemala; the many thousand local trees and recent sizable plantings are apparently free of the pathogen. The fungus was found in Guatemala in the 1950's as a pathogen of cinchona, however (7). Cuba, Puerto Rico, and Hawaii are other possible sources of *P. cinnamomi* for California; Cuba and Puerto Rico have had Phytophthora root rot problems on avocado for many years, although this crop has not been under cultivation as long nor is it as abundant in these countries as in Mexico and Central America.

If *P. cinnamomi* is not a native inhabitant of Latin America, a prime question is how the pathogen came to this hemisphere. If the pathogen is indigenous to the Malaysian-eastern Australian region, it may have been carried with plant material throughout the Pacific Islands on various trade routes and then on voyages to the Americas beginning in the 16th century. *Phytophthora cinnamomi* could have been introduced into Hawaii, Mexico, some of the other Latin American countries, Puerto Rico, and Cuba in voyages from the southern Asian and Australian areas.

On avocado and other hosts in California, our *P. cinnamomi* isolates are all of the A^2 mating type, with one exception (22), and are similar phenotypically to Rands' type culture from cinnamon in Sumatra. The A^2 isolates from avocado as well as the type culture from cinnamon are pathogenic to other hosts. Thus the A^2 type could have been brought into California on avocado seed or seedlings from Mexico in the later 1800's or early 1900's, primarily into avocado nurseries and ornamental nurseries, and then spread extensively through commercial avocado and ornamental plantings. *Phytophthora cinnamomi* apparently was spread to the San Francisco bay area and Halfmoon Bay in California on diseased heather (*Erica* spp.) plants from southern California nurseries (23). All of our collections of *P. cinnamomi* from Mexico and other countries in Latin America are of the A^2 type, and generally are phenotypically similar to the type culture from cinnamon in Sumatra. Our isolates from Hawaii vary considerably, though some are similar to the type culture.

The A^1 type from *P. cinnamomi*, on the other hand, probably came to California with camellia nursery stock from the southeastern United States. This is the only type that we have isolated from camellia in California, and is the only type found on camellia in North Carolina and Georgia (Zentmyer, *unpublished*). It could have been introduced into California with camellia stock from the southeastern USA, then spread to other areas from southern California nurseries (23, 24). Although camellia isolates are pathogenic to avocado, camellia was not the source of the major *P. cinnamomi* population on avocado in California; only one of our numerous avocado isolates from California is the A^1 mating type.

In relation to the origin of *P. cinnamomi*, Brasier's (1) recent paper on the ecological implications of the "Trichoderma effect," whereby species of *Trichoderma* stimulate oospore production only in the A^2 mating type of *Phytophthora*, is of interest. Of similar significance is the stimulation of oospore production in A^2 types by a substance in avocado roots (18). All of my cultures of *P. cinnamomi* from Latin America are A^2 mating type. With the preponderance of A^2 types in most parts of the world (22), including the Australian-Malaysian area, the opportunities for the introduction of this type into various Latin American countries have been greater than for introduction of the A^1 type. Another aspect of this is

that by responding with oospore production to *Trichoderma* or the substance in avocado root extract, the A^2 types are better adapted for survival than the A^1 types which have no such sexual mechanism. Perhaps A^1 types have been introduced into Latin America but have not been able to survive as well as the A^2 mating type.

Several of the species of *Persea* from which root samples have been taken in a native situation in Latin America are highly resistant to *P. cinnamomi* (20, 21). This resistance does not appear to have developed in the classical situation of pressure from the pathogen, based on my culture data to the present time.

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